are so oriented in most cases that they are as free to separate as if they were parallel rods. In early prophase there is some evidence of a coiled structure but in the later stages the shortening of the chromosomes is accompanied by a corresponding shortening of the chromonemata.

A comparison of the behavior of the chromosomes in *Secale*, *Lilium* and Orthopteran species indicates that the coiling of the chromonema is due to the difference between the rate of contraction of the chromosome and the chromonema. In grasshoppers the chromonema shortens as the chromosome contracts; in *Secale* the chromosome shortens rapidly in the prophase while the chromonema is practically unchanged in length, but at metaphase the chromosome is unchanged while the chromonema shortens; and in *Lilium* the chromonema shortens somewhat, but is always longer than the chromosome except when it is stretched out at early anaphase. Possibly the rate of division has something to do with these differences. In the two species of plants the stages from diplotene to late diakinesis are not easily obtained but in grasshoppers these stages are the most common. A rapid contraction of the chromosome might prevent the corresponding change in the chromonema while a relatively slow change in chromosome length and organization would permit the chromonema to accommodate itself to this change.

If the spiral chromonema is the result of a contraction of the chromatids held in a relatively fixed position, then they would be free to separate while still coiled as Kuwada describes for *Tradescantia*. In *Secale*, however, the paired chromatids do not separate while coiled and in *Lilium* the paired chromatids separate only when pulled apart at time of division of homologous chromosomes. In *Lilium* the chromonema between the spindle fibre attachments and the first chiasma, is usually straightened out before any split appears. Occasionally the distal ends of the chromonema separate while still coiled, but in most cases the chromatids appear to be closely associated and pull apart only under considerable tension. However, the coiling must be primarily of the type described by Kuwada, which is essentially the same as a corrugation in one plane, or the chromatids would be so entangled that they could not be pulled apart at metaphase. It is probable, however, that some twisting of the chromatids occurs so that they are not easily separated while coiled.

CHROMATID ASSOCIATION

In both plants and animals the most critical studies indicate that the meiotic chromosomes consist of four chromatids at diplotene. In some animals the four chromatids can be followed through the prophase stages and "tetrads" are commonly observed at diakinesis and at metaphase. Even in the more complicated ring formations in the Orthoptera the four chromatids can be identified.

In most plants, however, the tetrad nature of the chromosome cannot be seen until late metaphase when the homologous chromosomes are

practically separated. The failure to recognize the tetrad structure of plant chromosomes until the late stages of the first meiotic division is evidently due to the close association and coiling of the paired chromatids.

According to Darlington (1929), homologous chromosomes at diakinesis and metaphase are held together only through the exchange of partners between pairs of chromatids. The chiasmas formed by exchange of chromatids evidently do hold the paired chromosomes together at the earlier stages, but at diakinesis and metaphase the homologous chromosomes are often associated where no chiasmas are present. In *Datura* there are no chiasmas at the late stages of the first meiotic division and the chromosomes are associated only at the ends (Belling 1927). In *Secale* many metaphase chromosomes are attached at one end with no apparent chiasma formation (Figures 4, 5 and 6). In many cases the chromosomes are in contact at their ends with no evidence of the existence of earlier chiasmas. Apparently the chromonemata can be attached at their ends without exchange of partners between pairs of chromatids. In *Lilium* the chromosomes at metaphase are apparently held together only by their chiasmas. The difficulty of separation of homologues seems to be dependent on the number of chiasmas present at metaphase. In *Secale* there is no evidence of unusual tension in the separation of homologues but in *Lilium* the paired chromosomes are pulled apart with some difficulty. Darlington finds that the short chromosomes with a single chiasma separate earlier than long chromosomes with several chiasmas.

Darlington's study of polyploid Tulips and Hyacinths does show that the degree of pairing of homologous chromosomes is dependent on the number of chiasmas formed at diplotene. Only two chromosomes can be associated at any one point at pachytene so that in triploids the homologous chromosomes always change partners. At diplotene only two chromatids are associated at any one point and the exchange of partners among chromatids forms the only connection between two or more homologous chromosomes. Darlington's explanation of the method of chromosome and chromatid association is of considerable value in interpreting the mechanism of crossing over and the chromosome behavior in polyploid species.

In triploids the bivalents are apparently separated with some difficulty at the first meiotic division while univalents appear to divide readily in most cases. Newton and Darlington (1929) suggest that the difference in the behavior of bivalents and univalents in triploids may be due to the differences in the constitution of the chromatids. In a bivalent the chromatids in each homologue may be from different parents, due to crossing over, while in a chromosome which has not been paired they are of the same origin. Occasionally a univalent appears to divide like a bivalent, but such a univalent may have been associated with the bivalents at an earlier stage so that it might consist of chromatids from different chromosomes.